Identification of a QTL Associated with Tolerance of Soybean to Soil Waterlogging

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ABSTRACT

Soil waterlogging is a major environmental stress that suppresses soybean [*Glycine max* (L.) Merr.] growth and yield. Our objective was to identify quantitative trait loci (QTL) associated with the tolerance of soybean to soil waterlogging. We subjected 208 lines of two recombinant inbred (RI) populations, 'Archer' × 'Minsoy' and 'Archer' × 'Noir I', to 2 wk of waterlogging when the plants were at the early flowering stage. The control plants were not flooded. The experiment was conducted in three environments: Columbus, OH, in 1997 and 1998 and Wooster, OH, in 1998. We identified a single QTL, linked to marker Sat_064, from the Archer parent which was associated with improved plant growth (from 11–18%) and grain yields (from 47–180%) in waterlogged environments. This highly significant QTL ($P = 0.02$–0.000001) was identified in both RI populations and at both Columbus 1997 and 1998 environments, but not at the Wooster 1998 environment. The differences in soil type and flooding treatment (stagnant versus moving water) could have contributed to the lack of QTL identification at the Wooster 1998 environment. The Sat_064 QTL was uniquely associated with waterlogging tolerance and was not associated with maturity, normal plant height or grain yields. The Sat_064 marker maps close to the *Rps*4 gene for Phytophthora (*Phytophthora sojae* M.J. Kaufmann & J.W. Gerdemann) resistance; however, since Archer does not contain the *Rps*4 resistance allele, it is probably not a disease tolerance QTL. Near isogenic lines with and without the Sat_064 marker have been developed and are being field tested under waterlogging conditions to confirm the association of the QTL with the tolerance of soybean to waterlogging stress.

Periodic flooding during the growing season adversely affects soybean growth and grain production in many areas of the USA and the rest of the world. (Stanley et al., 1980; Oosterhuis et al., 1990). Soil can become flooded when it is poorly drained or when rainfall or irrigation is excessive. Other terms, such as soil saturation, waterlogging, anoxia, and hypoxia are also commonly used to describe flooding conditions. Flooding causes premature senescence which results in leaf chlorosis, necrosis, defoliation, reduced nitrogen fixation, and cessation of growth and reduced yield (Daugherty and Musgrave, 1994; Linkemer et al., 1998; VanToai et al., 1994; Bacanamwo and Purcell, 1999). In general, there are two types of flooding: waterlogging, where the root and a portion of the shoot are flooded, and complete submergence, where the entire plants are under water. Soil waterlogging for as little as 2 d reduced soybean yield by 18% at the late vegetative growth stage and 26% at the early reproductive stage (Scott et al., 1989).

In the last two decades, a great deal of information has accumulated from research on the molecular, biochemical, physiological, anatomical, and morphological responses of plants to flooding and anoxia (Kennedy et al., 1992; Perata and Alpi, 1993; Ricard et al., 1994; Crawford and Brandle, 1996; Vartapetian and Jackson, 1997). While the lack of oxygen has been proposed as the main problem associated with flooding (Ponnamperuma, 1972; Trought and Drew, 1980), growth reduction and yield loss during and after flooding could also arise from root rot diseases (Schmitthenner, 1985), nitrogen deficiency (Fausey et al., 1985), or nutrient imbalance (Hendry and Brocklebank, 1985; Thomson et al., 1989; Barrick and Noble, 1993). Recently, the accumulation of root zone CO_2 has been implicated as a cause of flooding injuries in soybean (Boru et al., 1997).

While the ability to produce high seed yield in flooded fields is the ultimate criterion of flooding tolerance, other traits, including leaf color, plant height, root, and shoot biomass, have been used frequently as determinants of flooding tolerance (Daugherty and Musgrave, 1994). However, attempts to apply this knowledge to the development of flood-tolerant crop cultivars have not yet been successful. Having elite high-yield soybean cultivars that are flood tolerant will reduce year-to-year yield variation and greatly benefit farmers. Genetic variability for flooding tolerance exists in soybean (VanToai et al., 1994). Tolerance to flooding in wheat (*Triticum aestivum* L.) and rice (*Oryza sativa* L.) is a quantitative trait controlled by a small number of genes (Boru et al., 2001; Setter et al., 1997). Xu and Mackill (1996) identified a random amplified polymorphic DNA (RAPD) marker that accounted for 50% of the variation in submergence tolerance of rice. The result was confirmed by an amplified fragment length polymorphism (AFLP) marker which mapped to the same area (Nandi et al., 1997).

During the last few years, molecular marker aided-selection has been used successfully for the breeding of crops with improved quantitative traits (Stuber, 1994). The objective of this research was to identify the QTLs associated with waterlogging tolerance of soybean. Mo-

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Abbreviations: ANOVA, analysis of variance; CO97, 1997 Columbus environment; CO98, 1998 Columbus environment; QTL, quantitative trait loci; RIL, recombinant inbred lines; WO98, 1998 Wooster environment.

lecular markers linked to these can be identified and be used to facilitate the development of flood-tolerant elite soybean cultivars by molecular plant breeding.

MATERIAL AND METHODS

Genetic Materials

One hundred twenty-two recombinant inbred lines (RIL) of the Archer × Minsoy and 86 RIL of the Archer × Noir I populations were used in this study. Archer is more tolerant to waterlogging than Minsoy and Noir I. The lines were selected from a larger set of RIL with maturity (group II or later) as the sole selection criterion. The populations were developed by Dr. Levi Mansur and had been inbred for nine generations. Each of the parents and RIL were characterized for the parental alleles with over 600 genetic markers including morphological traits, restriction fragment length polymorphism (RFLP), AFLP, and simple sequence repeats (SSR) (Cregan et al., 1999; Orf et al., 1999).

Field Experiments

Location and Soil Type

The study was conducted at the Ohio State University Waterman farm at Columbus, OH, in 1997 (CO97) and 1998 (CO98) and at the Ohio Agricultural Research and Development Center Snyder farm at Wooster, OH, in 1998 (WO98). The Waterman farm is located at latitude 39°59′N, longitude 83°01′W, and elevation 240 m. The soil type is a Kokomo silty clay loam (fine, mixed, mesic Typic Argiaquolls) with moderately slow permeability. The Snyder farm is located at latitude 40°47′N, longitude 81°55′W and elevation 306 m. Its soil type is a poorly drained Canfield silt loam (fine-loamy, mixed, mesic, Aquic Fragiudalfs).

Experimental Design and Statistical Analysis

The overall design of the experiment was a split-plot with the flooding treatments (i.e., waterlogged and control) as the whole-plot factor and genotypes assigned to sub-plots. In each of the three environments there was a single waterlogged field and an adjacent control field. Thus, environments served as replicates for the flooding treatments. At both locations, the waterlogged treatment was applied to a field that was leveled prior to the beginning of the study in 1997. In this field, the topsoil was removed and the sub-soil leveled to within ±3 cm. The topsoil was then reapplied and leveled. At Columbus, the leveled field was large enough to allow crop rotation. Half of the leveled field was used in the 1997 flooded treatment, while the other half was used in the 1998 flooded treatment.

Within each flooding treatment, genotypes were arranged in an augmented randomized complete block design. At Columbus, there were 15 blocks in 1997 and 17 in 1998. Each block consisted of 20 plots, of which five were assigned the parents and check cultivars (Archer, Minsoy, Noir, 'IA2007', and 'Conrad'), and the remaining 15 were assigned individual RI lines. Of the two checks, IA2007 was a breeding line with flooding tolerant potential, while Conrad is an Ohio standard public cultivar. A few extra genotypes not related to this experiment were added in 1998, accounting for the 16th and 17th blocks. At Wooster, there were 18 blocks, each with 18 plots. In each block, there was one plot of each parent or check (Archer, Minsoy, Noir, and IA2007). The remaining 14 plots were allocated to individual RI lines. Use of an augmented design for genotypes allowed us to estimate an experimental error, based on the replicated checks and parents, for each combination of environment and flooding treatment.

Planting dates were 7 May 1997 and 2 June 1998 at Columbus and 15 May 1998 at Wooster. Plots consisted of a single row, 1 m long, with 40 plants per row. Row spacing was 75 cm. No fertilizer was used, based on soil tests. Herbicides were applied as needed.

Flooding Treatment

The plants were subjected to soil waterlogging for 2 wk when 50% of the RI lines were at the early flowering (R1) growth stage (Fehr and Caviness, 1977). At the Columbus site, soil waterlogging was imposed by overhead irrigation and subirrigation (Fausey, 1994) to raise the water table to 5 to 10 cm above the soil surface. At the Wooster site, soil waterlogging was imposed by overhead irrigation alone. The control plots were irrigated as needed to avoid drought stress.

Soil Analysis

At each sampling time (before, during and after flooding), six soil samples were randomly collected in each plot to approximately 0.18-m depth with a 2.5-cm diam soil probe. The samples from each plot were combined, air dried, ground and analyzed for pH (1:1 water) (McLean, 1982). Soil chemical analyses to determine P, K, Ca, and Mg concentrations were conducted as described by Warncke and Brown (1998) at the Service Testing and Research Laboratory, Ohio Agricultural Development and Research Center, Wooster, OH.

Determination of Flooding Tolerance

Flooding responses were determined by plant growth and seed yield. To determine growth, plant height was taken just before flooding at about 8 wk after planting (early plant height) and 1 d after the flooding stress was removed (late plant height). At Columbus, maturity of each plot was recorded as the number of days after 31 July when 95% of the pods had reached their mature color. Maturity was not determined at the Wooster site. At the end of the season, the seeds were harvested by hand and seed yield determined.

Data Analysis and Mapping of QTL

Each of the environment-flooding treatment combinations was analyzed first as an augmented design to obtain genotype means, adjusted for blocks. We did not attempt to analyze the waterlogged and control portions of the full experiment in a single analysis. Rather, phenotypic means for waterlogged and control traits were mapped separately, with the idea of identifying markers that indicated QTL for traits under waterlogged conditions but that had no effect in the control condition.

Combined analysis of the three environments was complicated by heterogeneity of error across environments, which was apparent for all traits except maturity. To account for this, we used a mixed model analysis with location as a random factor and genotype as a fixed factor. For the diagonal of the variance-covariance matrix we used the error variance for each location, divided by the number of replications for the genotype in question (i.e., the number of blocks for a check or parent, 1 for a RI). Generalized least squares means for each RI, across locations, were used for mapping and correlation analysis. Correlation analysis was performed by SAS Software Package (SAS Institute Inc., Cary, NC) to quantify the degree of positive or negative linear relationship between the average trait means under flooded and nonflooded conditions.

Mapping was carried out for each location separately, with block-adjusted means. QTL for tolerance to soil waterlogging were identified and analyzed for interactions by the Epistat computer program (Chase et al., 1997). This computer software uses maximum likelihood methods and permutation tests for both the identification and evaluation of significance of interactions between pairs of QTLs (Chase et al., 1997). The simple interval mapping feature of the computer package PLABQTL (Utz and Melchinger, 1996), was also used for detecting QTL. This program uses a multiple regression approach to interval mapping with marker order and distances determined by MapMaker (Lander et al., 1987; Lincoln et al., 1993).

The empirical LOD thresholds for QTL detection was established using permutation tests (Churchill and Doerge, 1994). The Minsoy × Archer cross consists of 102 plants genotyped with 370 markers. The single marker threshold estimated to give a false positive rate of 0.05 was LOD 3.18; *P*-value 0.00066. The threshold for interactions was estimated at LOD 4.4; *P*-value 0.00004. The Noir × Archer cross consists of 75 plants genotyped with 347 markers. The single marker threshold estimated to give a false positive rate of 0.5 was LOD 3.17; *P*-value 0.00066. The threshold for interactions was estimated at LOD 4.4; *P*-value 0.00004. No significant interaction was detected.

RESULTS

Weather Conditions

At the Columbus site, the average temperature for the 1997 growing season from May 1 to September 30 was 17.6°C and was 1.3°C lower than the 20-yr historical average temperature (18.9°C). The 68.6 cm of total precipitation for the 5-mo growing season was 7.9 cm higher than the 20-yr historical precipitation. In 1998, the average temperature for the 5-mo growing season was 20°C which was 1°C warmer than the historical average, while the total precipitation of 35.8 cm was much lower than the historical precipitation of 60.7 cm. In 1998, the average temperature of the Wooster site was 18.5°C and was 1.1°C warmer than the historical average of 17.3°C. 1998 was also a dry year for the Wooster site with a total precipitation of 48.0 cm as compared with the historical precipitation of 56.1 cm.

Effects of Waterlogging

Responses of the parents and IA2007 to the waterlogging treatment are reported in Table 1. The average maturity of Minsoy and Noir I in the control treatment was similar, but Archer matured 10 to 15 d later ($P = 0.05$). Waterlogging did not alter the maturity of Archer and Minsoy but hastened the maturity of Noir I by 6 d ($P = 0.05$). Similarly, waterlogging also hastened the maturity of IA2007 by 8 d ($P = 0.05$).

The average early plant height of all the genotypes was significantly shorter (13 to 15%) in the flooded plots than in the control plots across the three environments (Table 1). Since early plant height was determined before the flooding treatment, plants in the flooded plots were probably under some form of stress (i.e., soil compaction due to land leveling) independent of the flooding stress.

Waterlogging for 2 wk at the flowering stage significantly reduced the late plant height of Minsoy by 16%, of Noir I by 23% and of Archer and IA2007 by 27 and 28%, respectively, as compared with the nonflooded plant height.

The effects of waterlogging were much more severe on grain yield than on plant height. Waterlogging for 2 wk reduced grain yield of Archer the least (69%), followed by Minsoy (75%), while the grain yield of Noir I was reduced by 84% relative to control yield. The grain yield of IA2007 was reduced by 77% after 2 wk of flooding.

The correlation between control grain yield and flooded grain yield was not significant across the two populations and three environments (Table 2). The correlation between late plant height and grain yield was significant ($P = 0.05$) but smaller in the control ($R = 0.32$) than in the waterlogged treatment ($R = 0.53$). The correlation between maturity and grain yield was significant in the control treatment ($R = 0.23$), but not significant in the waterlogged treatment ($R = 0.16$).

Mapping of QTL for Tolerance to Waterlogging

A single marker, the Archer allele of Sat_064, was identified to associate with flooding tolerance in the combined data of the Archer × Minsoy population across all three environments (Table 3). The Sat_064

Table 1. Average responses of the three parents, check line and the two RI populations to flooding and control treatments at three environments.

Variety	Maturity			Early height				Late height				Yield			
	CO97	CO98	Mean	CO97	CO98	WO98	Mean	CO97	CO98	WO98	Mean	CO97	CO98	WO98	Mean
	d after July 31			cm				cm				g plot^{-1}			
								Flooded							
Archer	34	41	37	26	26	25	26	39	60	56	52	95	165	126	129
Minsoy	22	32	27	22	27	25	25	25	42	45	38	5	67	103	61
Noir 1	19	26	22	28	29	28	28	35	51	54	47	11	53	70	52
Archer × Minsoy	36	40	38	21	25	25	24	31	51	55	35	42	117	98	86
Archer × Noir 1	33	39	36	24	26	25	25	36	57	58	50	42	89	113	81
IA2007	38	45	41	20	27	25	24	30	66	62	51	48	224	157	114
LSD_{05}	2	2	6	2	2	1	1	4	5	5	4	17	45	22	19
								Control							
Archer	40	39	39	33	31	27	30	66	79	68	71	537	453	346	413
Minsoy	26	26	26	30	31	27	29	39	46	55	45	110	235	241	248
Noir 1	27	28	28	39	33	30	33	55	69	60	61	316	337	302	334
Archer × Minsoy	43	40	42	29	29	27	28	57	75	63	65	338	403	327	356
Archer × Noir 1	39	39	39	32	29	22	28	68	78	68	71	496	430	340	422
IA2007	51	47	49	27	27	27	28	66	72	79	71	616	406	458	495
LSD_{05}	1	1	5	3	2	2	2	7	6	8	5	83	71	40	42

Table 2. Correlation of different trait means under flooded and control conditions across two populations and three environments.

	Flooded				Control			
	Maturity	Early height	Late height	Yield	Maturity	Early height	Late height	Yield
					Flooded			
Maturity								
Height Before	0.29*†							
Height After	0.33*	0.55*						
Yield	0.16	0.31*	0.53*					
					Control			
Maturity	0.53*	0.01	0.08	0.11				
Height Before	0.09	0.43*	0.46*	0.12	−0.22*			
Height After	0.29*	0.24*	0.47*	0.11	0.11	0.45*		
Yield	0.28*	−0.15	−0.03	<−0.01	0.23*	0.13	0.32*	1.00

† The correlation coefficients with the asterisks are significant at the probability levels of <0.05.

marker was highly associated with grain yield (P = 0.00066) and late plant height (P = 0.00008) of the waterlogged treatment. The effect of this allele in the Archer × Noir I population across all three environments was also highly significant on grain yield (P = 0.0001) and late plant height (P = 0.00466) of waterlogged plants. When the results of each environment were analyzed separately, the effect of Archer Sat_064 allele was highly significant in both populations at the CO97 and CO98 environments. Its effect, however, was not detected at the WO98 environment in either population.

In the CO97 environment, waterlogged plants of the Archer × Minsoy population which had the Archer Sat_064 allele produced 100% more grain (58 g/row) than plants without the allele (28 g/row) (Table 4). The waterlogged plants which had the allele also were 17% taller (34 cm) than plants without the allele (29 cm). In the Noir I × Archer population, the presence of the allele increased the grain yield and late plant height of the waterlogged plants by 180% and 18%, respectively, as compared with the waterlogged plants without the allele.

Similar results were also detected in the CO98 environment. In the Archer × Minsoy population, plants with the Archer Sat_064 allele produced 54% more grain yield and were 18% taller after waterlogging than plants without the allele. In the Archer × Noir I population, the presence of the allele improved the grain yield of waterlogged plants by 47% and late plant height by 11% as compared with plants without the allele.

The Archer Sat_064 allele was not associated with any other traits that were determined in the waterlogging treatment including flooded maturity and flooded early plant height. The allele was also not associated with grain yield, maturity, early plant height, or late plant height of the control treatment.

DISCUSSION

A single QTL marked with Sat_064 was associated with taller plant and greater grain yield of waterlogged plants of both RI populations in both years (1997 and 1998) at the Columbus location. The fact that the same QTL affected both growth and grain yield under waterlogged conditions indicated that plants that grew better during the 2-wk waterlogging stress (i.e., taller) also produced more grain at the end of the growing season. Flooded plant height has been used as indicator of flooding tolerance (Daugherty and Musgrave, 1994). This study confirms the relatedness (R = 0.53) between flooded plant height and flooded grain yield (Table 2),

Table 3. Probability of the association of the Sat_064 marker with different traits in the Archer × Minsoy and Archer × Noir 1 populations at three environments.

Treatment	Trait	Columbus 97	Columbus 98	Wooster 98	Overall
			Archer × Minsoy		
Flooded	**Yield**	0.00002†	0.00012	0.250	0.00066
	Maturity	0.31300	0.04200	NA	0.05500
	Early Height	0.17600	0.16800	0.410	0.45000
	Late Height	0.00016	0.00180	0.190	0.00008
Control	**Yield**	0.171	0.593	0.249	0.52600
	Maturity	0.131	0.269	NA	0.13500
	Early Height	0.206	0.704	0.483	0.45200
	Late Height	0.389	0.076	0.893	0.14100
			Archer × Noir 1		
Flooded	**Yield**	0.000001	0.01594	0.576	0.00010
	Maturity	0.982000	0.73200	NA	0.80600
	Early Height	0.232000	0.32600	0.833	0.25100
	Late Height	0.000800	0.02900	0.513	0.00466
Control	**Yield**	0.160000	0.37900	0.495	0.20000
	Maturity	0.680000	0.69700	NA	0.66800
	Early Height	0.439000	0.35400	0.831	0.61300
	Late Height	0.660000	0.58600	0.241	0.82000

† Values that are underscored are significant based on the single marker threshold estimated by permutation test. The single marker threshold estimated to give a false positive rate of 0.05 was LOD 3.18; P-value 0.00066 for the Archer × Minsoy population and LOD 3.17; P-value 0.00066 for the Archer × Noir 1 population.

Table 4. Trait means of lines in the Archer × Minsoy and Archer × Noir I populations which either have (A) or lack (B) the Archer Satxx064 allele.

Treatment	Trait	Columbus 97 A	Columbus 97 B	Columbus 98 A	Columbus 98 B	Wooster 98 A	Wooster 98 B	Overall A	Overall B
					Archer × Minsoy				
Flooded	Yield (g · row^{-1})	58**†	29**	148**	94**	93	103	94**	77**
	Maturity (d after July 31)	36	36	41	40	na	na	39	38
	Early Height (cm)	22	21	26	25	24	25	24	24
	Late Height (cm)	34**	29**	55**	48**	56	54	48**	44**
Control	Yield (g · row^{-1})	340	300	397	408	311	326	353	360
	Maturity (d after July 31)	43	41	41	40	na	na	42	41
	Early Height (cm)	29	28	28	29	27	27	28	28
	Late Height (cm)	58	56	78	72	62	62	67	64
					Archer × Noir I				
Flooded	Yield (g · row^{-1})	70**	25**	113**	77**	109	117	104**	78**
	Maturity (d after July 31)	33	33	39	39	na	na	36	36
	Early Height (cm)	25	24	27	26	25	25	25	25
	Late Height (cm)	40**	34**	60**	54**	57	59	53**	49**
Control	Yield (g · row^{-1})	469	514	425	448	334	346	391	410
	Maturity (d after July 31)	39	39	39	38	na	na	39	39
	Early Height (cm)	33	32	31	30	28	28	30	30
	Late Height (cm)	68	67	78	77	66	68	71	71

† This means with the asterisks within each environment are significantly different at the probability levels of <0.01.

the ultimate criterion of flooding tolerance in production agriculture. However, while Sat_064 was a strong marker which explained from 22 to 33% of the variation in grain yield of the two populations, it only explained 8 to 9% of the variation in flooded plant height (Table 4).

The Sat_064 marker was specific for flooding tolerance and was not associated with growth and grain yield under nonflooded, control conditions. The Sat_064 marker is mapped to the linkage group G of the USDA soybean linkage map (Cregan et al., 1999). The *Rps*4 gene for Phytophthora resistance is also mapped to the same position linkage group. While Archer contains the *Rps*1k and *Rps*6 genes, it does not contain the *Rps*4 gene. In addition, no visible disease symptoms were detected in the CO97 and CO98 environment. Nevertheless, the possibility that the Sat_064 QTL is associated with the tolerance of a flooding related disease cannot be ruled out. Indeed, some preliminary linkage data suggest that *Rps*6 is located in the vicinity of the Sat_064 allele (Demirbas et al., 2001)

The fact that the Sat_064 QTL was not identified at the Wooster site was perplexing. The flooding treatment at the Columbus site was imposed by subirrigation to raise the water table from below the ground. During the flooding treatment, the water was stagnant. At the Wooster site, flooding was imposed by continuous overhead irrigation. The flooded plots at that site were on high ground and water was constantly moving through the soil profile during the flooding treatment. According to Heatherly and Pringle (1991), stagnant flooding was more injurious to soybean growth and yield than flooding with moving water. It has been documented that the low-lying areas of many fields are usually highly compacted due to the loss of soil structures resulting from farm machinery traffic on wet soil (Fausey and Lal, 1990). Natural flooding that occurs in these areas is probably more similar to the flooding stress at the Columbus site than at the Wooster site.

While the Sat_064 effect was detected in both populations and in both CO97 and CO98 environments, the effects of the QTL on flooded grain yield and plant height were much larger in the CO97 environment than in CO98 environment. After the field leveling in 1997, soil of the flooded plots in Columbus was highly compacted as indicated by the depressed growth and yield. The flooded plots were deep plowed in the spring of 1998 before planting which significantly improved grain yield. It is possible that the Sat_064 QTL was associated with depressed growth and yield due to compacted and flooded soil.

Flooding did not change the soil P, K, Ca, and Mg concentrations at either Columbus or Wooster. However, the soil at the Columbus site was one pH unit higher and contained three to four times more P, K, Ca, and Mg than the soil in Wooster (Table 5). Since the overall flooded yield at the WO98 environment was not different from that at the CO98 environment, soil fertility was probably not a determining factor affecting the identification of the flood-tolerance QTL at that site.

In summary, we have identified a QTL that is associated with tolerance of soybean to flooding and soil compaction. The QTL was highly significant and accounted for 47 to 180% increase in grain yield in flooded, compacted soil. The fact that the QTL was identified in both

Table 5. Soil chemical analysis of the Columbus 1998 and Wooster 1998 environments.

Environment	Treatment	Sampling time†	pH	P	K	Ca	Mg
				mg kg^{-1}			
Columbus							
	Control	Before	7.1	220	335	2510	430
	Control	After	7.4	292	325	2310	401
	Flooded	Before	7.1	275	381	2410	420
	Flooded	During	7.3	253	384	2630	498
	Flooded	After	7.2	275	359	2440	426
Wooster							
	Control	Before	6.2	65	98	1120	136
	Control	After	6.3	66	124	850	130
	Flooded	Before	6.1	59	90	850	123
	Flooded	During	6.2	54	103	930	156
	Flooded	After	6.4	74	116	1250	187

† Relative to the flooding treatment.

the Archer × Minsoy and Archer × Noir I populations and in two environments indicated that this QTL was not a statistical artifact. Using marker-aided selection, we have developed near isogenic lines (NIL) which either have or lack the Archer Sat_064 allele. These lines are being field tested under compacted and waterlogged soil conditions to confirm the association of the QTL to flooding tolerance of soybean.

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